DEVELOPMENT OF THE DIGITATELY DECOMPOUND LEAF IN CUSSONIA SPICATA (ARALIACEAE)

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EVEN THOUGH LEAF FORM is one of the earliest and most common characteristics used in descriptions of plants, the interpretation of the leaf form in most species of *Cussonia* has still to be clarified. These include South African *Cussonia* species such as *C. spicata* Thunb., *C. sphaerocephala* Strey, *C. arenicola* Strey, *C. nicholsonii* Strey, *C. zuluensis* Strey, and *C. gamtoosensis* Strey.

In all six species the leaves have long petioles and are digitately compound, with 5 to 13 digits radiating from a single point, the compacted rachis. These digits are homologous to the pinnae of a pinnately compound leaf. Since each digit is further once or several times vertebrately divided, the entire leaf is thus digitately decompound.

At the present time interpretations of what the parts of each digit represent vary. For example, Strey (1973) refers to an individual digit as a "vertebrate leaflet" consisting of pinnules arranged along a winged rachilla. In contrast, Van der Schijff (1971) divides each digit (pinna) into leaflets of the first, second, and third order.

In order to clarify this problem, the external morphology of the leaf of *Cussonia spicata* was studied at progressive stages of development. Since the leaf form of *C. spicata* varies considerably, the form that appeared to be the most complex was examined. This would make interpretation of less complex leaf forms relatively easy.

MATERIALS AND METHODS

Leaves of *Cussonia spicata* are formed in clusters at the apex of branches during a growth flush. As a result, all stages of leaf development are present in a single actively growing shoot apex. Such shoot apices were fixed in formalin-acetic-acid-alcohol and examined under a dissection microscope. All apices were collected from one plant growing in the Loskop Dam Nature Reserve in the Northern Transvaal (*W. F. Reyneke, 280*), where specimens of this plant occur in quite large numbers. The leaves of these plants differ from those of other members of *C. spicata* in that they have a considerably more complex form and are gray-green in contrast to the dark green leaves of other plants in the same and other localities.

OBSERVATIONS

The leaf development of *Cussonia spicata* can be divided into two phases: (1) the development of the digitately decompound leaf in its entirety and (2) the development of an individual vertebrately (de-)compound digit.

Development of the digitately decompound leaf

Following the initiation of the pyramidal leaf primordium (Figure 1A), limited apical growth occurs while the two stipular primordia differentiate laterally. At this stage the leaf primordium is approximately 230 μm. long (Figure 1B) and comprises a median petiolar-midrib region (Foster, 1936) and two lateral stipular primordia.

The stipular primordia develop rapidly, so that at a very early stage they are already very much wider and longer than the petiolar-midrib region. During their development the young stipules extend toward each other behind the petiolar-midrib region, and the leaf axis then lies against the stipules (Figure 1C–G).

As in the leaf development of most Angiospermae, the apex (tip) of the petiolar-midrib region matures very early, and when the leaf axis is approximately 300 μm. long, the first digit primordia have already been initiated (Figure 1C). The initiation of the digit primordia resembles that of the pinnae in most pinnately compound leaves, which arise basipetally as a result of localized marginal growth. Since the future rachis of the digitately decompound leaf is reduced or compacted in *Cussonia spicata*, the digit primordia appear to emerge at the same level (Figure 1D). A single apical digit primordium (I), which is homologous with the apical leaflet of imparipinnate leaves, develops first. This is followed by two lateral digit primordia (II, II^1), and the subsequent pairs of lateral digit primordia (III, III^1, IV, IV^1, etc.) are formed on either side of the preceding pair in a similar manner. Eventually this leads to an uneven number of digits in a mature leaf (Figure 4), with the single apical digit (I) the oldest and the most lateral pair the youngest. The apical digit (I) and the first pair of lateral digits (II and II^1) usually are at maturity the most complex, while the digits most laterally situated are less complex. In some leaf forms of *Cussonia spicata*, the most lateral digits can even be simple.

Immediately after their initiation, the first five digit primordia lie in the same vertical plane, but as the leaf matures, more digits are initiated anteriorly on either side of the first five digit primordia. The young leaf then eventually has its digits arranged in a semicircle around the reduced rachis, with the adaxial surfaces of the digits facing one another. It is because of this arrangement that the first differentiated digit is often referred to as the posterior or central digit and the last differentiated digits as the anterior or most lateral digits.

The further development of a single digit was studied using the posterior digit from leaves of different ages.

Development of the vertebrately (de-)compound digit

Once the digit primordium has reached a length of about 0.5 mm. (Figure 1F), it elongates rapidly. Apical growth here is also of short duration, and the first pair of lateral leaflets soon appear as rod-shaped structures on the adaxial leaf surface (Figure 1G). Their appearance is

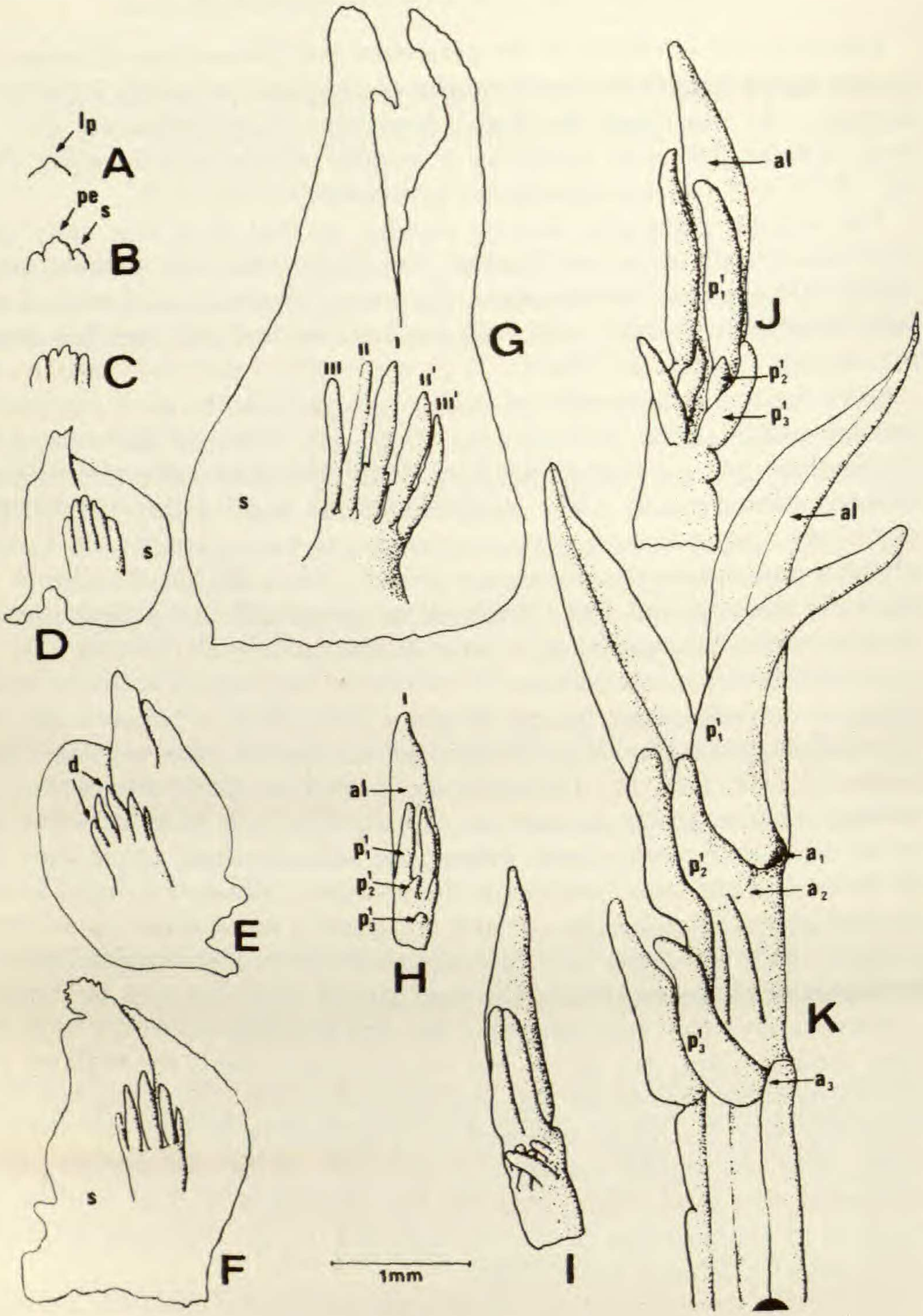

FIGURE 1. A–G. Different stages in the development of the digitately decompound leaf of *Cussonia spicata* (abaxial surface): A, initiation of pyramidal leaf primordium (lp); B, differentiation of two stipular primordia (s) on either side of the petiolar-midrib region (pe); C, initiation of digit primordia at the apex of the petiolar-midrib region. D–G. Further development of the young stipules and digit primordia (d); I, II, II^1, III, and III^1 show the sequence in which the digits initiate. H–K. Different stages in the development of a single digit (adaxial surface): a_1 = articulation no. 1; a_2 = articulation no. 2; a_3 = articulation no. 3; al = apical part of digit primordium; p_1^1 = first leaflet pair of first gene = ration at articulation no. 1; p_2^1 = second leaflet pair at articulation no. 2; p_3^1 = third leaflet pair at articulation no. 3.

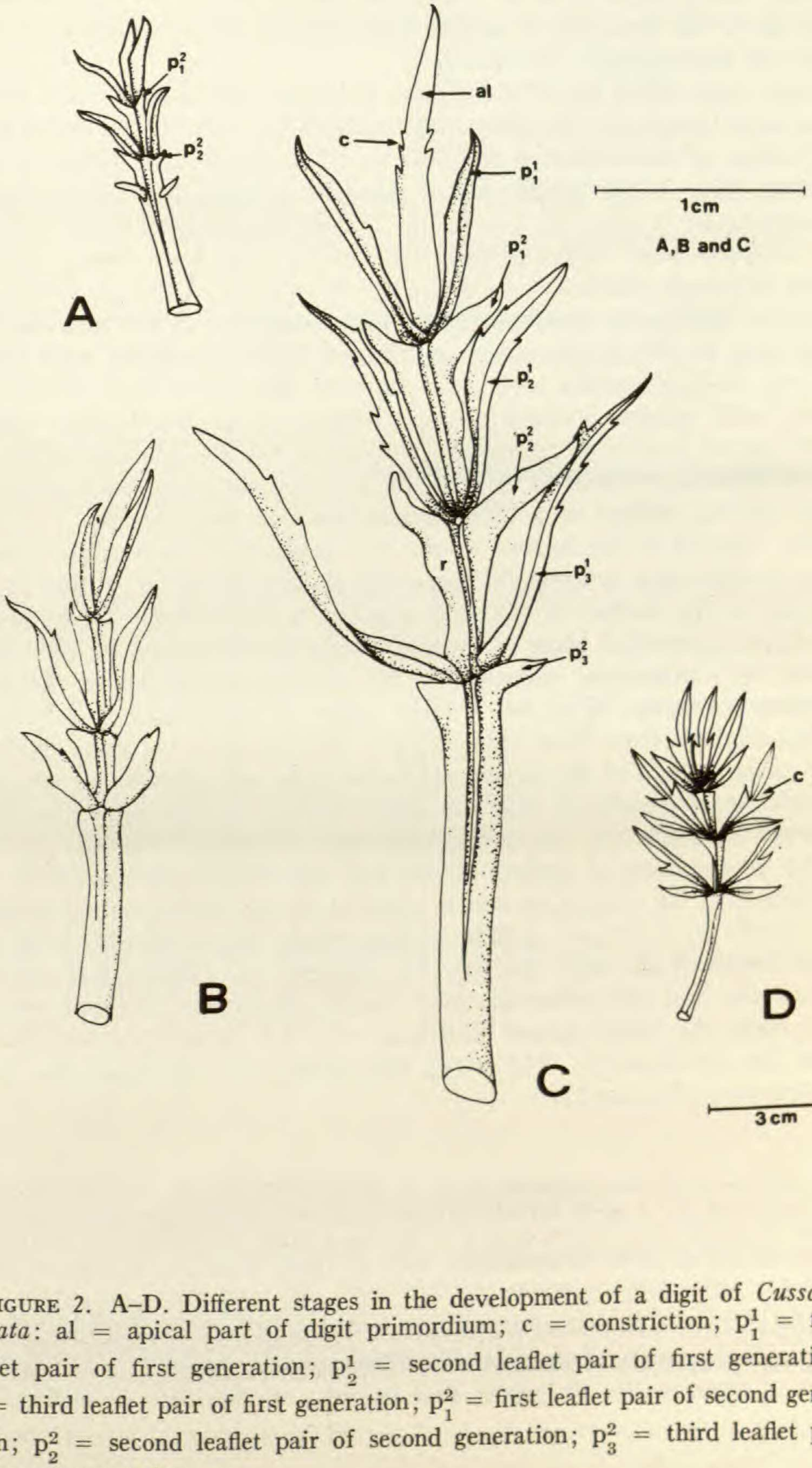

FIGURE 2. A–D. Different stages in the development of a digit of *Cussonia spicata*: al = apical part of digit primordium; c = constriction; p_1^1 = first leaflet pair of first generation; p_2^1 = second leaflet pair of first generation; p_3^1 = third leaflet pair of first generation; p_1^2 = first leaflet pair of second generation; p_2^2 = second leaflet pair of second generation; p_3^2 = third leaflet pair of second generation.

followed by the basipetal differentiation of an additional one or two pairs of leaflet primordia (FIGURE 1H). These lateral pairs of leaflets on the digit are called leaflets of the first generation and are able to subdivide by forming constrictions (FIGURE 2D). The apical part of the digit primordium above the first pair of lateral leaflets gives rise to an apical leaflet which can also constrict (FIGURE 2C).

Those parts where the different pairs of lateral leaflets of the first generation arise basipetally are termed articulations 1, 2, and 3, i.e., leaflet pair no. I arises at articulation 1 and pair no. II arises at articulation 2, etc. (FIGURE 1K). If the apical part of the digit primordium does constrict, the articulation is called no. 4 (FIGURE 3) and a pair of lateral leaflets may even originate here. Although only four articulations have been observed during this study, there may be up to five in some digits (Strey, 1973).

During subsequent development a rapid elongation of the rachilla and an increase in size of the apical and lateral leaflet primordia take place (FIGURE 1I–K), together with a flattening of these structures. When the young leaflet reaches a length of approximately 1 cm., the lateral leaflets of the second generation appear and develop at the articulations, with the leaflets directly proximal to those of the first generation, and according to Strey (1973), leaflets of a third generation may even develop (FIGURE 2A-D). Similar to the leaflets of the first generation, these second generation leaflets arise in basipetal succession at articulations 1, 2, and 3. In contrast to the leaflets of the first generation, which arise as distinctly rod-shaped primordia, those of the second generation appear to have been formed by a prominent widening of the rachilla directly below the articulations (FIGURE 2C). At a later stage of development individual leaflets originate from these widened parts (FIGURE 2D). At some articulations these leaflets of the second generation may not constrict at all, may constrict incompletely, or may not even develop. Leaves have also been observed on which only one of a possible pair of leaflets develops.

The development of leaflets of the first and second generations is accompanied by an elongation and broadening of the digit axis and eventually results in a winged rachilla. These wings, which extend along the entire length of the digit, are not only between articulations but are also beyond the first and below the most basal articulations (FIGURE 3). In most cases the wings appear V-shaped, with the broadest part directly below the articulations. The wings themselves can sometimes also form constrictions (FIGURE 3).

CONCLUSION AND SUMMARY

According to these observations, it is apparent that the development of the digitately decompound leaf of *Cussonia spicata* corresponds, in general principle, to that of a pinnately compound leaf. In *Cussonia*, however, apical growth of the petiolar-midrib region ceases at a very early stage. Consequently, the digits that develop on this axis emerge at the

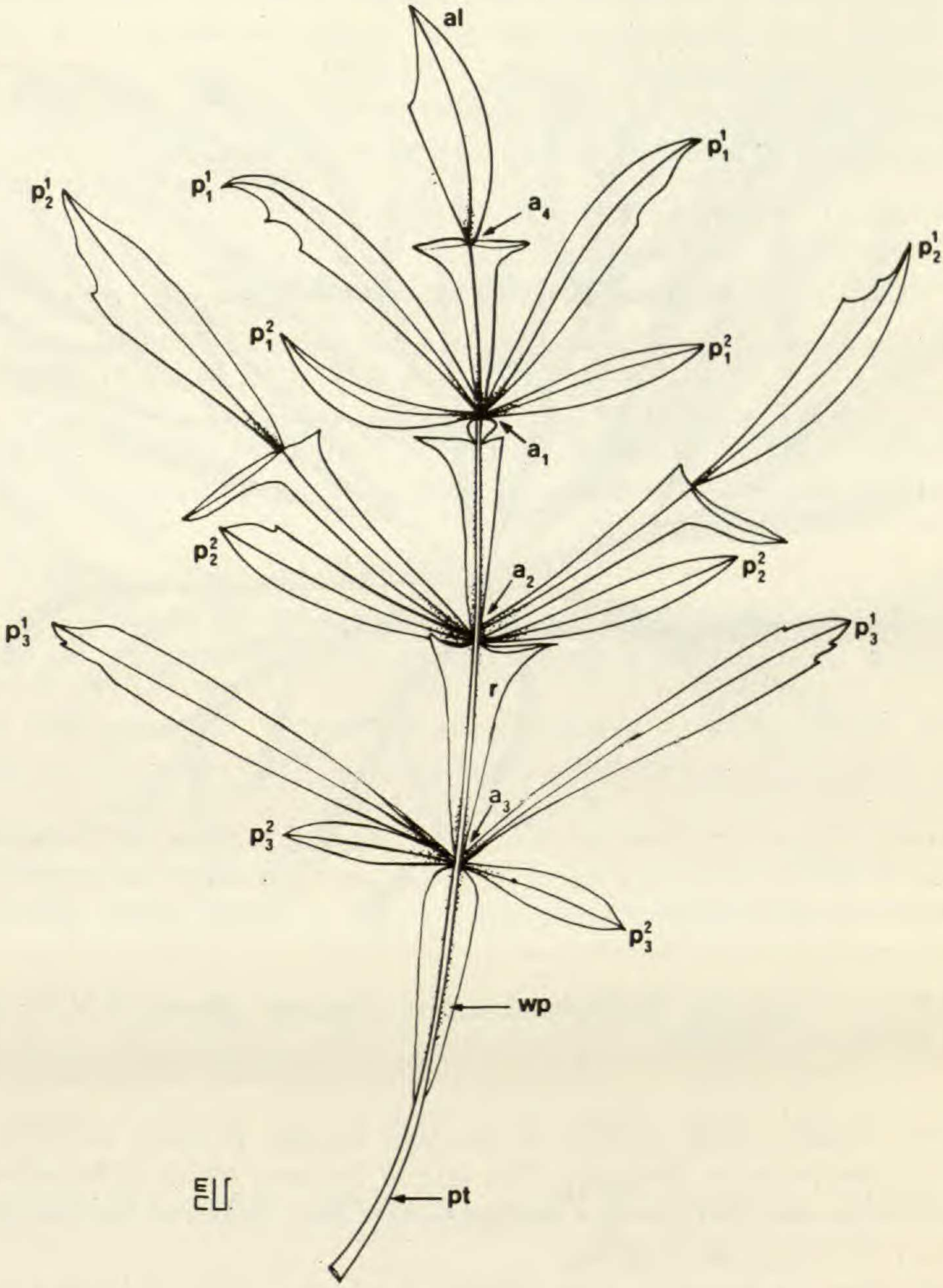

FIGURE 3. Fully developed digit: a_1 = articulation no. 1; a_2 = articulation no. 2; a_3 = articulation no. 3; a_4 = articulation no. 4; al = apical leaflet; p_1^1 = first leaflet pair of first generation; p_2^1 = second leaflet pair of first generation; p_3^1 = third leaflet pair of first generation; p_1^2 = first leaflet pair of second generation; p_2^2 = second leaflet pair of second generation; p_3^2 = third leaflet pair of second generation; pt = petiolule; r = winged rachilla; wp = winged petiolule.

same level, thus resulting in a palmate arrangement of digits about the reduced rachis (FIGURE 4).

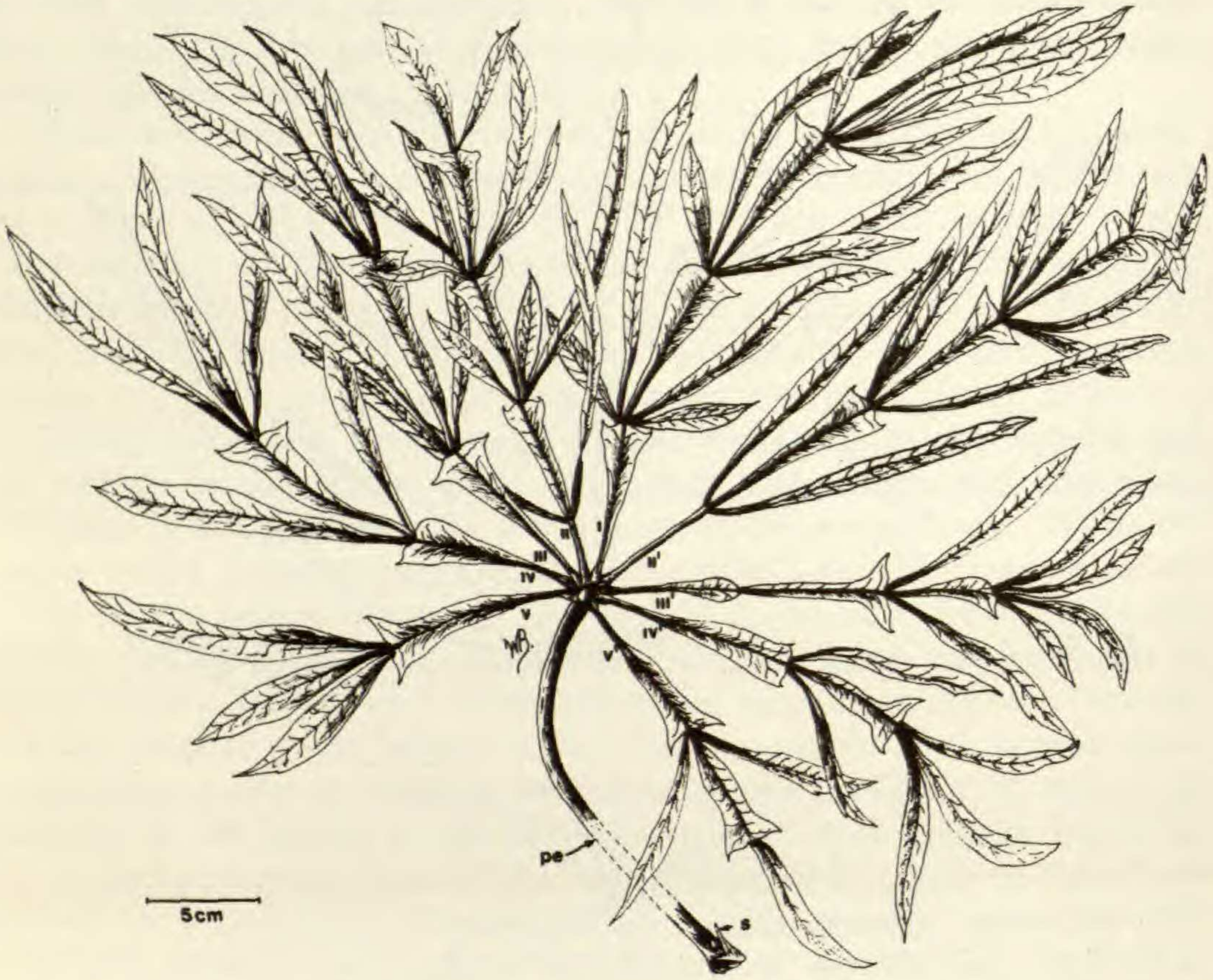

FIGURE 4. Digitately decompound leaf of *Cussonia spicata*: I–V = digits; pe = petiole; s = stipules.

Even though apical growth of the digit is also of short duration, the rachilla continues to elongate. The lateral leaflets, which differentiate at the different articulations in a basipetal direction, therefore become spaced at intervals along the rachilla.

The shape of the entire fully developed leaf of *Cussonia spicata* is digitately decompound, with the different digits (homologous with the pinnae of a pinnately compound leaf) arranged palmately about the reduced rachis. The individual digits vary in complexity. The posterior or central digit, which differentiates first, is the most complex, while the anterior or most lateral digits, which develop last, are the least complex. There is a gradual decrease in complexity from the apical leaflet to the most lateral leaflets. Although most digits are vertebrately compound, the apical digit, as well as those adjacent to it, may be vertebrately decompound, while the most lateral digits may be simple. Depending on the complexity of the digit, one or two generations of lateral leaflets differentiate basipetally at articulations along the rachilla, resulting in a vertebrately compound digit.

In some cases the lateral leaflets of the first generation may constrict, thus forming a vertebrately decompound digit.

Although leaf development has not been investigated in other species of *Cussonia* with compound leaves, their leaf development does appear to correspond quite closely to that of *C. spicata*. In most other species of *Cussonia* the mature leaf is not as complex as in *C. spicata*, since there is usually only one articulation, no articulation, or occasionally no leaflets of the second generation at all.

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